Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE SOUND-TRANSMITTING APPARATUS OF SALAMANDERS AND THE PHYLOGENY OF THE CAUDATA

E. R. DUNN

SMITH COLLEGE

RESEARCHES by Kingsbury and Reed, extending through a number of years, have shown that the sound-transmitting apparatus of salamanders consists of two elements. These are the columella and the operculum.

In the most recent paper on this subject, Reed (1920) gives a résumé of all the previous work, an extensive account of the state of affairs in the *Plethodontidæ,* a brief account of the conditions in other forms, and the findings are presented in the form of a family tree.

The purpose of the present article is to add an account of the condition of the apparatus in two forms not seen by Reed, to question the condition described by Kingsbury and Reed for *Dicamptodon ensatus* (*Ambystoma tenebrosum* Auct.), to suggest a somewhat different interpretation of the facts observed by them, and to propose a somewhat different phylogeny, which seems to agree quite as well with the otic apparatus and far better with other anatomical features.

Kingsbury and Reed (1909) were unable to examine any of the Asiatic forms related to *Hynobius.* These forms, as Cope pointed out long ago, are rather different from the *Ambystomidæ,* with which they have usually been associated, and should in fact form a family *Hynobiidæ.*

I have recently been able to examine large series of *Hynobius leechii* from Korea. This animal shows a condition of the otic apparatus different from any seen by Kingsbury and Reed, and a condition which I am compelled to consider primitive. Both columella and operculum are present as free and distinct elements. Both are readily movable. There is a m. opercularis.

I have not been able to examine skulls of *Onychodactylus,* or of *Ranodon.* Okajima's (1908) figures of *Onychodactylus* show only one element which is in appearance much like that of *Cryptobranchus.* This is very different from the appearance of the apparatus of *Hynobius.* It is evident that either fusion of operculum and columella has taken place or that the operculum has not developed. *Onychodactylus* is partly aquatic, a mountain brook animal. *Cryptobranchus,* which, as I shall show later, is a derivative of the *Hynobiidæ,* has failed to develop the operculum. Probably the same is true of *Onychodactylus* and of *Ranodon* as well, although for the latter Wiedersheim's (1877) figure is all we have. Still, as Kingsbury and Reed (1909) say, his Fig. 67 "suggests a condition such as is found in *Cryptobranchus.*"

Rhyacotriton olympicus was not examined by Kingsbury or by Reed. This animal (Dunn, 1920) possesses both columella and operculum. The columella is free from the periotic and is readily movable. The operculum is little developed. The animal is in part aquatic, a mountain brook species.

Dicamptodon ensatus was examined by Kingsbury and Reed (1909), and while my dissection of an adult showed the state of affairs which they describe, I can not follow them in calling it "much like that in the adult *Ambystoma.*" In adult *Ambystoma* the columella is solidly fused to the periotic. A bony operculum nearly fills the opening of the fenestra, and is attached by a membrane around its circumference. In *Dicamptodon,* on the other hand, about half of the fenestra is filled by the plate of the columella, and the remainder by cartilage. The cartilage extends around the plate of the columella. There is nothing that could be called a definite operculum. If the cartilage is called the operculum, then the columella and operculum are fused and the operculum is fused to the ear capsule by nearly its whole border. It seems to me that in this case the columella is at least more free than in *Ambystoma*, and the operculum less developed. This would be in line with what is known of the habits of *Dicamptodon*. It is a much more aquatic animal than is *Ambystoma*.

In the Caudate sound-transmitting apparatus, taking Reed (1920) as a basis, there are the following sets of conditions:

I. Both columella and operculum present. Both free.
Hynobius, Rhyacotriton.
II. Operculum not developed. Columella free.
Cryptobranchus.
Megalobatrachus Ranodon ?,
Onychodactylus ?, Dicamptodon ?
III. Operculum developed, free. Columella fused to periotic, stylus present.
Salamandra, Ambystoma.
IV. Operculum developed, free. Columella fused to periotic. Stylus absent.
Triturus, Pachytriton, Pleurodeles ?,
Tylototriton ?.
V. Operculum developed, free. Columella ?.
Siren, Batrachoseps.
VI. Both columella and operculum present, fused together, free from periotic.
Necturus.
VII. Both columella and operculum present. Fused together. Operculum attached by narrow fusion to periotic.
Amphiuma, Plethodontidæ
(exc. *Batrachoseps*).

Inasmuch as II is a condition found also in larvæ, there is no reason to suppose that the animals in which this condition occurs form a natural group.

Condition V has been commented upon by Reed (1920), and I am fully in accord with his ideas in this connection. *Siren* and *Batrachoseps* are certainly not related. Both are extremely specialized. *Batrachoseps* has certainly passed through stage VII. *Siren* has certainly passed through an ancestral period of terrestrial life, yet its other peculiarities are such that it is dangerous to state that its relationships are with the forms in stage IV.

The forms which show condition VI and condition VII form what Reed (1920) calls Legion II, as distinct from the forms which show conditions I–V (exc. *Batrachoseps*), which Reed calls Legion I.

But the sound-transmitting apparatus of *Necturus* agrees with that of *Amphiuma* and the *Plethodontidæ* only in having the columella and operculum fused. There is no reason to suppose that such a fusion may not have occurred twice, especially as the details of the fusion in *Necturus* differ somewhat from the manner in which the fusion occurs in *Amphiuma* and the *Plethodontidæ*. In *Necturus* the columella forms a goodly part of the plate-like portion of the apparatus. In the forms of condition VII, the plate-like portion is almost entirely composed of the operculum, and the columella is represented by the stylus. In this case the evidence of the ear bones is non-committal. Considered apart from all other features of the anatomy condition VII might equally well be derived from condition VI or both independently from condition I. But, as we shall see, evidence from other features of the anatomy precludes our regarding *Necturus* as intervening between the *Plethodontidæ* and the other Mutabilian forms.

It is extremely interesting to note that Reed has found almost exactly the same state of affairs in *Amphiuma* and in the *Plethodontidæ*. The exact relationships of *Amphiuma* have long been in dispute, and while I prefer to be conservative about the position of the animal, I think it extremely likely that further evidence will show that it is closer to the *Plethodontidæ* than it was placed in the older classifications.

Any classification should be based upon all available characters, so that possible parallelisms will not lead to wrong conclusions. In the present instance we are dealing with a stock neither absolutely terrestrial nor absolutely aquatic. From this stock there have been several branches which have become more aquatic and several which have become more terrestrial. Excellent examples of this are the numerous incursions into a mountain brook habitat, with the penalty of loss or reduction of lungs. The list is extensive, *Onychodactylus*, *Rhyacotriton,* four species of *Triturus, Salamandrina, Chioglossa,* all the stock of the *Plethodontidæ,* an assemblage representing four families. The sound-transmitting apparatus is admittedly correlated with the mode of life. Therefore as a character in determining relationships it must be used with extreme caution.

The following outline classification of salamanders does not counter any of the facts concerning the otic apparatus, and is based on many characters.

As regards the *Plethodontidæ* and the *Hynobiidæ,* revisions of both are nearly completed, based on the examination of some 8,000 specimens of the first family and 1,000 of the second.

The *Sirenidæ* are the most isolated group. Scarcely a character can be found to ally them with one or another of the main stocks. The pelvis is gone, the skull is that of a very specialized larva, the hyoids are those of almost any larva, the tail vertebræ are very different from those of any other salamander, inasmuch as there is no hæmal arch. There are flat plates on each side which do not meet in the mid-ventral line. There is no prearticular.

The *Proteidæ* are only slightly less isolated. The pelvis differs in having an anterior median projection and no ypsiloid apparatus. The skull is larval. The branchial arches are reduced from the primitive larval quota. The prearticular is absent.

The *Amphiumidæ* also have modified larval branchial arches, and the pelvic girdle lacks the ypsiloid apparatus. But *Amphiuma* has an adult skull which resembles remotely that of the *Salamandridæ.* The otic apparatus is that of the *Plethodontidæ.* There is no prearticular bone. It is quite possible that this genus is descended from primitive Salamandrids.

The others have directly comparable skulls, branchial arches, and pelves, and in dealing with their relationships we are on much firmer ground.

Several characters divide them into two series, which should, I think, rank as superfamilies.

1. Prearticular bone. Present in *Cryptobranchidæ* and *Hynobiidæ*, and absent in *Ambystomidæ*, *Salamandridæ* and *Plethodontidæ*.
2. Second epibranchial. Present in *Cryptobranchidæ* and *Hynobiidæ*, and absent in *Ambystomidæ*, *Salamandridæ*, and *Plethodontidæ*.
3. First ceratobranchial and first epibranchial fused into a single cartilaginous rod in *Cryptobranchidæ* and in *Hynobiidæ*. Separate elements in *Ambystomidæ*, *Salamandridæ* (exc. *Salamandra*, where all parts fuse), and *Plethodontidæ*.
4. Nasals meeting in median line and premaxillæ without nasal process in *Cryptobranchidæ* and *Hynobiidæ*. Nasals separated by nasal spines of premaxillæ in *Ambystomidæ*, *Salamandridæ*, and *Plethodontidæ* (exc. *Pseudotriton*, where nasals overlap premaxillary spines).
5. Pubotibialis muscle fused with puboischiotibialis in *Cryptobranchidæ*. The two muscles are separate in all other salamanders (Noble, 1922). I have ascertained that the two are fused in *Hynobius* and in *Onychodactylus*.
6. Larvæ of *Ambystomidæ*, *Salamandridæ*, and *Plethodontidæ* have the first ceratobranchials fused with the second basibranchial (Smith, 1920). This fusion does not occur in larvæ of *Cryptobranchidæ* or of *Hynobiidæ*.

Within the superfamily *Salamandroidea* the *Ambystomidæ* and the *Salamandridæ* are about parallel. The long posterior process of the prevomer distinguishes the *Salamandridæ*, and as the parasphenoid tooth patches of *Plethodontidæ* are the morphological equivalent of this process (Wilder, 1920) it is probable that some primitive Salamandrid (having the two otic elements free) gave rise to the much degenerate *Plethodontidæ*. The mountain brook habitat of the ancestral Plethodontid (Wilder and Dunn, 1920) accounts perfectly for the retention of the columella through adult life as a working part of the sound-transmitting apparatus.

The *Cryptobranchoidea* contains two families. Of these the *Hynobiidæ* is the more primitive. The *Cryptobranchidæ* differ in lacking the lachrymal bone, in the larval position of the vomerine teeth, and in the much depressed form of the body and head, the last two evidently adaptations for aquatic and bottom-living habits. Besides the characters mentioned in the list as aligning the *Cryptobranchidæ* with the *Hynobiidæ*, several minor points also show this relationship. Both *Ranodon* and *Hynobius* frequently have a lateral fold between the insertions of the legs. This is very prominent in both *Cryptobranchus* and in *Megalobatrachus*, and is not found elsewhere. *Onychodactylus* larvæ have a marked fold on the posterior side of the limbs. This is seen elsewhere only in *Cryptobranchus* and in *Megalobatrachus*.

Inasmuch as the characters differentiating the two genera of *Cryptobranchidæ* have not been clearly understood in the past they are here stated.

Megalobatrachus,	Two persistent branchial arches: Frontal not entering naris: Branchial clefts closed in adult.
Cryptobranchus,	Three persistent branchial arches: Frontal entering naris: Branchial clefts open in adult.

In all three of these characters the American genus shows greater adaptation to aquatic life. The European fossils of this family appeal to *Megalobatrachus* in the one skull character which separates the two genera. Neither in *Andrias schuchzeri* nor in *A. tschudii* does the frontal enter the naris.

It is also interesting to note that *Megalobatrachus* shows no "Derotreme" characters whatever, although in the older classifications it was included in the *Derotremata*.

The extreme antiquity of the *Caudata* can be readily seen when an end form, a river adaptation, is found in Oligocene times.

This of course puts the origin of the main stocks back at least to the end of the Mesozoic, a conclusion to which the distribution also forces us.

The primitive characters appear in widely scattered and rather unrelated forms. The free prearticular has already been mentioned. A free lachrymal is found in *Hynobiidæ* and in an Ambystomid, *Rhyacotriton.* A postfronto-squamosal arch is found in one group of the *Salamandridæ.* A T-shaped parasphenoid is found in an Ambystomid (*Dicamptodon*) and in a Salamandrid (*Tylototriton*). Long maxillæ are found in the two forms just mentioned and in another Salamandrid, *Pachytriton.* Posteriorly projecting prevomers are found in *Amphiuma,* in all *Salamandridæ,* in some *Hynobiidæ* (*Hynobius, Pachypalaminus*), and to a less extent in *Dicamptodon.*

All these are theoretically primitive skull characters of amphibians. Their appearance separately in diverse forms is sufficient indication that the three families *Hynobiidæ, Salamandridæ,* and *Ambystomidæ,* while containing all the more primitive forms of the order, stand in no direct genetic relationship to each other, but must be derived from a more or less remote common stock which combined the otic apparatus, lachrymal, and prearticular of *Hynobius* with the long maxilla, T-shaped parasphenoid, and postfronto-squamosal arch of *Tylototriton.*

The evidence of Paleontology, as far as it goes, supports this view. I intend in a later paper to assemble the meager facts regarding fossil salamanders. These facts, it may be here stated, lend no support to the prevalent view that the *Proteida* are an old, a primitive, or an ancestral group.

The following outline classification indicates the size and position of the modern groups. The genera and species of the *Salamandridæ* are probably not wholly accurate. Future work will perhaps indicate the affinities of *Amphiuma,* the *Proteidæ,* and the *Sirenidæ.*

Of the larger families, the *Hynobiidæ* are entirely Asiatic, the *Salamandridæ* are Eurasiatic with four American species, the *Plethodontidæ* are American with two species in Europe and four in South America, and the *Ambystomidæ* are American with one Asiatic species. As the Northern land masses have been connected with each other during Tertiary times this distribution is not extraordinary, although close resemblance between widely separated species is eloquent testimony as to the antiquity of some of the "modern" forms.

Twenty-two of the recognized genera and 105 of the species are restricted to North America, 13 genera and 56 species are Eurasiatic, while three genera are found both in North America and in some parts of the Old World.

Mutabilia
  Salamandroidea
    1. Ambystomidæ ....3 genera, 16 species.
      Dicamptodon 2, *Rhyacotriton* 1, *Ambystoma* 13.
    2. Salamandridæ ....7 genera, 37 species.
      Salamandra 5, *Chioglossa* 1, *Tylototriton* 2, *Pachytriton* 1, *Pleurodeles* 3, *Triturus* 24, *Salamandrina* 1.
    3. Plethodontidæ ....16 genera, 83 species.
      Desmognathus 7, *Leurognathus* 1, *Plethodon* 11, *Ensatina* 3, *Hemidactylium* 1, *Aneides* 4, *Batrachoseps* 6, *Stereochilus* 1, *Typhlotriton* 1, *Typhlomolge* 1, *Gyrinophilus* 2, *Pseudotriton* 5, *Eurycea* 10, *Hydromantes* 3, *Œdipus* 23, *Œdipina* 4.
  Amphiumoidea (Relationships uncertain, possibly should stand as a family under Salamandroidea)
    4. Amphiumidæ ....1 genus, 2 species.
      Amphiuma 2.

Cryptobranchoidea
5. Hynobiidæ ....5 genera, 20 species.
Hynobius 15, *Pachypalaminus* 1, *Onychodactylus* 2, *Ranodon* 1, *Batrachuperus* 1.
6. Cryptobranchidæ ....2 genera, 2 species.
Megalobatrachus 1, *Cryptobranchus* 1.

Proteida (Relations uncertain)
7. Proteidæ ....2 genera, 3 species.
Necturus 2, *Proteus* 1.

Meantes (Relationships uncertain)
8. Sirenidæ ....2 genera, 2 species.
Siren 1, *Pseudobranchus* 1.

Total number of genera 38, of species 165.

LITERATURE CITED

Dunn, E. R. 1920. Notes on Two Pacific Coast Ambystomidæ. *Proc. New England Zool. Club*, VII, pp. 55–59.

Kingsbury, B. F., and Reed, H. D. 1909. The Columella Auris in Amphibia. *Jour. Morph.*, XX, pp. 549–628.

Noble, G. K. 1922. The Phylogeny of the Salientia. Part I. The Osteology and the Thigh Musculature, their Bearing on Classification and Phylogeny. *Bull. Amer. Mus. Nat. Hist.*, XLVI, pp. 1–87.

Okajima, K. 1908. Die Osteologie des *Onychodactylus japonicus*. *Zeitschr, wiss. Zool.*, XCI, 3, pp. 351–381.

Reed, H. D. 1920. The Morphology of the Sound-transmitting Apparatus in Caudate Amphibia and its Phylogenetic Significance. *Jour. Morph.*, XXXIII, pp. 325–375.

Smith, L. 1920. The Hyobranchial Apparatus of *Spelerpes bislineatus*. *Jour. Morph.*, XXXIII, pp. 527–550.

Wiedersheim, R. 1877. Der Kopfskelet der Urodelen. *Morph. Jahrb.*, III, pp. 352–548.

Wilder, I. W. 1920. The Urodele Vomer. *Anat. Record*, XVII, p. 349.

Wilder, I. W., and Dunn, E. R. 1920. The Correlation of Lunglessness in Salamanders with a Mountain Brook Habitat. *Copeia*, 84, pp. 63–68.